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Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker

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Abstract

Arthropod diversity, abundance and biomass on 50–70-year-old longleaf pine (*Pinus palustris*) tree boles were examined to determine the origin of the prey available to the endangered red-cockaded woodpecker (*Picoides borealis*) and the variability of this prey over time. Traps designed to capture arthropods crawling on the bark (crawl traps), alighting on the bark (flight traps), and crawling on the ground (pitfall traps) were operated continuously for 12 months. Flight and crawl traps were placed at different heights. One-half of the trees with crawl traps were fitted with a barrier to prevent arthropods from crawling up from the ground. Arthropods were identified to genus from one weekly sample per month and subsamples were oven-dried and weighed to estimate biomass. The arthropod community on the bark included over 400 genera. Crawl trap captures were the most similar to the prey of *P. borealis*. Arthropod fauna captured in crawl traps had a 58% similarity to pitfall trap captures and a 60% similarity with flight trap captures. Flight and pitfall trap captures had a 10% similarity. Barriers to arthropod movement up the tree reduced the arthropod biomass on the bole of the trees by 40–70%. Arthropod biomass was relatively evenly distributed over the tree, but varied seasonally with the highest biomass captured in the fall of the year. In general, the study showed that little of the arthropod biomass on the bark is in the form of arthropods that live exclusively in that habitat and that a large portion of the biomass is crawling up from the soil/litter layer. © 1998 Elsevier Science B.V.

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1. Introduction

A number of bird species take advantage of the arthropod resource that occurs on the bark of trees. One of these, the endangered red-cockaded woodpecker primarily forages on the bark of live southern pines (Ligon, 1968; Morse, 1972; Nesbitt et al., 1978; Hooper and Lennartz, 1981; DeLotelle et al., 1983; Porter and Labisky, 1986). This species shows a preference for trees larger than 25 cm diameter at breast height (DBH) and rarely forages on trees less than 30 years old if older trees are available. It nests and roosts in cavities constructed in live trees and forms social groups composed of a breeding male

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and female and non-breeding helpers (Walters, 1990). Because constructing cavities in lives trees requires considerable effort (Baker, 1971b; Jackson et al., 1979; Carter et al., 1989), a red-cockaded woodpecker group remains in the same area as long as the habitat is suitable (Ligon, 1970).

Efforts to increase red-cockaded woodpecker populations and improve their habitats have had a major impact on forest management practices on public lands within its range, including national and state forests and military reservations. Maintaining or improving the foraging habitat surrounding cavity tree clusters is one of the most controversial parts of these management efforts (McConnell, 1995). Current foraging habitat management guidelines were developed from data on red-cockaded woodpecker breeding success on the Francis Marion National Forest in South Carolina (US Fish and Wildlife Service, 1985).

Information about arthropods found on the bark of living trees is limited. Jackson (1979) characterized the bark as a 'bedroom community' where arthropods lay eggs or overwinter but do little else, but more recent studies show that macroarthropods use the tree bole in a variety of ways. Moeed and Mead (1983) conducted the most extensive study of arthropods on the bark of four tree species in New Zealand and found that the tree bole is an important pathway to the canopy for many arthropods. Nicholai (1986) studied the physical properties of the bark and the resident arthropod fauna of six deciduous tree species in Germany. In the Pacific Northwest of the United States, Mariani and Manuwal (1990) studied arthropods on the bark of living Douglas fir (*Pseudotsuga menziesii*) in relation to brown creepers (*Certhia americana*) and found that brown creeper abundance was correlated with spider abundance on the bark. More recently, Hooper (1996) conducted a study of arthropods in bark crevices of longleaf pines (*Pinus palustris*) of varying ages during the winter in South Carolina and found that arthropod biomass on the bark was at its highest on 86-year-old trees. However, no data are available on which arthropods are associated with the bark of living southern pines during other seasons, how those arthropods vary seasonally or where they originate, so a study was conducted in 1992 and 1993 to answer those questions.

2. Materials and methods

2.1. Study area

The study was located on the Savannah River Site (SRS), an 80 269 ha US Department of Energy (DOE) nuclear production facility near Aiken, South Carolina. The SRS is within the upper Atlantic Coastal Plain Physiographic Province. Its northern sector consists of uplands and sandhills where conditions are dry and the most common plant communities are longleaf pine plantations and natural stands of longleaf pine and turkey oak (*Quercus laevis*). Loblolly pine (*P. taeda*) and bottomland hardwoods predominate on the more mesic and riparian areas. Longleaf, loblolly, and slash (*P. elliotii*) pine stands occupy approximately 14 924 ha, 25 677 ha and 12 011 ha, respectively (Knox and Sharitz, 1990). Most of the stands are under 50 years old. Potential red-cockaded woodpecker nesting habitat on the site is limited because only 1521 ha are in pine stands 60 years or older. The land surrounding the centrally located nuclear production areas is managed by the USDA Forest Service. One objective of forest management on the site is the recovery of the red-cockaded woodpecker.

Eight stands of mature (50–70-year-old) longleaf pine, managed for red-cockaded woodpecker foraging and nesting habitat, were selected for the study. The stands were widely distributed throughout the SRS.

2.2. Insect trapping

2.2.1. Flight traps

At each of the eight stands, nine dominant or codominant trees were selected to receive traps. One tree was randomly selected to receive flight-intercept traps to capture insects attempting to land on the tree bole. The flight-intercept traps are described in detail by New (1995). Briefly, the upper portions of the traps are constructed of plexiglass panels (21×30 cm). Plexiglass tops and sides (5 cm wide) are glued to the main panels to increase the likelihood of capturing strong flying insects that fly up or to the side when they hit a barrier. A triangular piece of aluminum sheet metal, painted black, is attached to the bottom of the trap and folded at the edges to help

funnel falling insects into the collection container. The top half of a plastic 1-l soft drink bottle is inverted and attached to the bottom of the trap as the collection container. This container is filled with approximately 200 ml of a preservative consisting of 1% formaldehyde in a saturated NaCl solution. Holes drilled in the side of the collection container prevent liquid overflow when it rains. Galvanized nails 6 cm long are hammered partially into the tree and the traps are hung from them by wire loops attached to the traps.

Fifteen flight-intercept traps were hung along the bole of the selected tree at each plot. On each tree, three flight-intercept traps were hung equally spaced around the circumference of the tree bole at 1, 4, 7, 10 and 13 m from the ground.

2.2.2. Crawl traps

The remaining eight trees were paired into four groups of two trees. Each group was randomly selected to receive crawl traps attached to the bole at either the base (1 m above the ground), mid-bole (half the distance between the ground and the first branches), base of the crown or middle of the crown. Three traps were attached equidistantly around the circumference of the bole at the designated position except at the mid-crown position where only two traps could be fitted on the bole.

Crawl traps are described by Hanula and New (1996). The traps consist of a modified metal funnel that is inverted, attached and sealed to the bark of the tree. A collection container is attached over the upturned spout of the funnel so that arthropods crawling up the tree move through the funnel and into the collection container where they are preserved in the same solution used in the flight-intercept traps. The funnels are painted black to reduce the likelihood that they will repel arthropods, and the inside of the funnel is treated with spray glue and sand to make it easier for arthropods to crawl up into the traps.

After the traps were in place, one tree from each group (trap position) was selected and fitted with a barrier placed approximately 0.5 m above the ground. The barrier was designed to prevent arthropods from crawling up the tree from the ground to determine how much of the arthropod community associated with the bark moves onto the tree from the forest floor/litter layer. The barrier consisted of a 7- to 8-cm wide band of aluminum sheet metal completely encircling the bole. The bark beneath the barrier was scraped smooth without injuring the tree to provide a tight seal when the barrier was in place. The barrier was held with one 3-cm long roofing nail and the lower edge was sealed with silicone caulk to prevent arthropods from crawling under it. The surface of the barrier was coated with Fluon (Northern Products, Woonsocket, RI), a polytetrafluoroethylene suspension, to create a slippery surface that most macroarthropods cannot crawl up.

2.2.3. Pitfall traps

Ten pitfall traps were placed on the forest floor in each plot to determine how much the forest floor and bark communities overlapped in composition. The pitfalls were laid out in two lines of five traps spaced 10 m apart within the lines. The lines were also 10 m apart.

The traps consist of a 480-ml capacity plastic cup with drain holes in the bottom that is buried in the soil so the top is even with the soil surface. A second collection cup filled with preservative solution is placed inside the first and a funnel is set inside the mouth of the larger cup so that arthropods are directed into the smaller cup. The funnel is coated with Fluon to prevent arthropods from crawling out once they enter the trap. Each trap is covered by a 15×15 cm piece of aluminum sheet metal supported by 20-cm long aluminum nails to reduce trap flooding by rainfall. The nails, inserted through holes on opposite edges of the cover, hold the cover approximately 5 cm above the trap.

2.3. Bark sampling

Bark samples were collected by scraping an area of bark 0.3×0.5 m at each sample location (Hooper, 1996). Bark from branches was collected by removing the bark from the entire circumference of the selected branch for a length of 1 m. For each tree, bark was sampled from the base, mid-bole, base of the crown, mid-crown, and from one live branch. An aerial lift truck was used to reach the higher locations. Samples were placed in plastic bags, stored at 4°C, and examined within one week of collection. All arthropods were removed and stored in 70%

ethyl alcohol until they were identified. Bark samples were collected from one tree stand^{-1} month^{-1} for 14 months.

In addition, one dead branch was collected per tree per plot during July, August and September 1993. The dead branches were placed in plastic bags and returned to the laboratory where they were broken apart with a hatchet and all arthropods were removed.

2.4. Sample handling

All insect traps were operated continuously and samples were collected weekly from September 1992 to September 1993. An aerial lift truck was used to retrieve samples from the upper bole and canopy to minimize the disturbance to the bark surface and prevent injuries to the trees that might attract insects. Samples were stored in 70% ethyl alcohol, sorted to morphologically similar groups and identified to genus or the lowest taxonomic level possible. Because the number of specimens collected in insect traps was large, only specimens from one weekly collection per month were identified. The weeks chosen for inclusion in the study coincided with the weeks bark samples were collected.

Arthropods were classified by ecological function or guild to determine which functional groups were dominant on the bark. Guilds were assigned based on feeding habits. In cases where larvae and adults had different habits, larval habits designated the guild. Guilds included: detritivores, herbivores aboveground, herbivores belowground, nectar and pollen feeders, predators, wood borers and omnivores.

2.5. Statistical analysis

Estimates of arthropod biomass were obtained by oven drying arthropods at 40°C for 72 h and weighing them. Twenty to 30 specimens of each genus were individually weighed to obtain an average weight per specimen which then was multiplied by the number of individuals collected to calculate an overall estimate of weight. Some genera had species that differed in size or consisted of immature and adult stages. In these cases, representatives of each size class were dried and weighed. If fewer than 20 specimens were collected, they were all dried and weighed. Specimens occasionally escaped during bark sampling. These were recorded with an estimate of the size and then the weight of a similar sized specimen was used to estimate biomass. Arthropods collected on the bark were grouped into seasonal categories of spring (April, May and June), summer (July, August and September), fall (October, November and December) and winter (January, February and March) to compare arthropod biomass and abundance over time.

The amount of faunal overlap between flight-intercept, crawl traps and pitfalls was calculated using Raabe's percent similarity (Southwood, 1966). This index determines the percentage of each taxa in a sample, compares two samples by individual taxa and determines the lowest common percent overlap for each taxa. These are then summed to calculate overall percent similarity. Comparisons were made between traps of the same type at different heights and between trap types.

Arthropod diversity was estimated with the Shannon index (H') (Shannon, 1948). The Shannon index measures diversity in terms of numbers of taxonomic classes present and the relative abundance of those classes.

Analysis of variance tested for differences in arthropod abundance and biomass among heights within trap types. In some cases, the data were transformed using $\log_{10}$ or square root transformations to stabilize the variance. Means were compared using the Ryan-Einot-Gabriel-Welch multiple F-test (SAS, 1985). A paired t-test (SAS, 1985) tested for differences in abundance and biomass in crawl traps at the same positions with and without a barrier restricting arthropod movement up the tree.

3. Results

3.1. Arthropod community

Pitfall traps in mature longleaf pine stands captured representatives of 266 arthropod genera from 146 families and 18 orders (Table 1). Hymenoptera, primarily Formicidae (ants), were captured most frequently (7397 specimens), but Diplopoda (millipedes), Coleoptera (beetles), and Orthoptera had the three highest cumulative biomasses.

Table 1
Total number and biomass of arthropods captured from the forest floor (pitfall traps) and the boles of live pines (crawl and flight traps) in mature longleaf pine stands during a 1-year period (September 1992–September 1993)[a]

Class of order	Pitfall		Crawl traps (no barriers)		Flight	
	Number	Biomass (g)	Number	Biomass (g)	Number	Biomass (g)
Araneae	538	4.67	1427	5.70	–	–
Coleoptera	1728	23.49	233	7.44	2179	15.31
Diplopoda	1061	49.17	9	0.33	–	–
Diptera	629	0.39	60	0.04	1310	0.789
Geophilomorpha	10	0.05	6	0.05	–	–
Hemiptera	67	1.08	185	3.73	112	3.410
Homoptera	69	0.06	445	0.28	454	0.735
Hymenoptera	7397	4.66	890	0.73	426	2.905
Isoptera	8	0.01	2	0.002	144	0.170
Lepidoptera	120	1.27	44	0.238	80	0.562
Lithobiomorpha	3	0.05	–	–	–	–
Mecoptera	11	0.08	–	–	–	–
Neuroptera	19	0.02	198	0.139	70	0.143
Orthoptera	283	16.2	222	5.52	63	1.457
Phalangida	96	0.81	93	0.402	–	–
Plecoptera	–	–	8	0.005	–	–
Psocoptera	6	0.001	363	0.033	1637	0.314
Scolopendromorpha	60	4.6	5	0.215	–	–
Thysanura	4	0.004	12	0.130	–	–

[a] Captures from 80 pitfall traps, 88 crawl traps and 120 flight traps. Traps were operated continuously but only 1 weekly sample month^{-1} was examined.

Crawl traps on trees without barriers to arthropod movement captured arthropods in 203 genera from 118 families. In contrast to pitfall traps, crawl traps captured high numbers of spiders (Araneae) and Hymenoptera (Table 1). Although abundant, Hymenoptera were low in biomass while Coleoptera, Araneae, Orthoptera and Hemiptera had high biomasses.

Flight traps tend to be biased toward clumsy fliers, e.g. the Coleoptera. Our flight traps were no exception, capturing 2179 beetles from 52 families and 151 genera (Table 1). Overall, flight traps captured insects from 144 families and 321 genera. Coleoptera, Hemiptera and Hymenoptera were the dominant orders in terms of biomass captured. The higher biomass of Hymenoptera in flight traps relative to other trap types was the result of captures of large species in the Apidae, Vespidae, and Sphecidae families.

We assigned arthropods to guilds based on published reports of their larval feeding habits. Pitfall trap captures were dominated numerically by omnivores with detritivores and predators also occurring in relatively large numbers (Table 2). However, a large portion of the arthropod biomass was in the detritivore guild in the Diplopoda and Orthoptera orders, particularly roaches and crickets.

The arthropod community that crawls on the bark surface was composed of high numbers of predators, omnivores, detritivores and herbivores (Table 3). Detritivore biomass was highest on the bark when adults of wood borers whose larvae inhabit dead trees were included in that guild. The most common detritivores on the bark were roaches (Orthoptera: Blattidae; *Parcoblatta* sp.). Two weevils, *Hylobius pales* and *Pachylobius picivorus*, classified as wood borers (detritivores) based on larval habits, were the greatest single source of detritivore biomass captured on the bark. Herbivores (root and foliage feeders) also made up a large portion of the biomass of the bark community as did predators. Omnivores, although numerically abundant, were primarily ants

Table 2
Total number and biomass (g oven-dried weight) of arthropods in various guilds captured in pitfall traps operated on the forest floor of eight mature longleaf pine stands from September 1992 to September 1993[a]

Guild	Number	Biomass (g)
Herbivore (above ground)	357	4.19
Herbivore (below ground)	15	0.07
Detritivore	2807	75.39
Wood borer	54	1.36
Predator	1550	21.62
Omnivore	7206	3.78
Pollen/nectar	15	0.05

[a] Captures from 80 pitfall traps. Traps were operated continuously but only 1 weekly sample month^{-1} was examined.

which had a relatively small cumulative biomass. Herbivore biomass was confined to a few large insects that included leaf-footed bugs (Hemiptera: Coreidae; *Acanthocephalus* sp.) and grasshoppers (Orthoptera: Acrididae; *Schistocera* sp.). Seventeen specimens of those two genera totalled over 8 g of the 12.8 g of herbivore biomass caught in crawl traps over a 1-year period.

Flight traps captured high numbers and biomasses of detritivores as well as herbivores that feed on aboveground or belowground portions of plants (Table 4). Predators also were abundant in flight traps. Wasps and beetles were the most abundant predators in these traps, while spiders were the most common predators in crawl traps.

3.2. Sources of bark arthropods

Comparison of arthropod diversity and faunal similarity in trap captures by height or position on the tree bole showed that trees with crawl traps plus a barrier to arthropod movement had fewer insects, but approximately the same number of arthropod genera and diversity as those without barriers regardless of the trap position along the bole (Table 5). Because percent similarity was also high (83.7%) between trees with and without barriers, the trees without barriers were utilized for comparisons of similarity with other trap types or among trap positions.

In flight traps, the number of genera declined with increasing height along the tree bole (Table 6). Despite the decline in the number of genera, the Shannon diversity remained relatively constant along the tree bole.

Table 3
Total number and biomass (g oven-dried weight) of arthropods in various guilds captured in crawl traps located at different heights on longleaf pine tree boles; one-half of the trees had barriers at their bases to prohibit arthropods from crawling from the ground onto the boles[a]

Guild	Base		Mid-bole		Base of crown		Crown	
	Number	Biomass (g)	Number	Biomass (g)	Number	Biomass (g)	Number	Biomass (g)
Trees without barriers								
Herbivore (aboveground)	149	1.55	239	1.63	155	4.19	98	0.65
Herbivore (belowground)	2	0.12	0	0	5	0.31	3	0.01
Detritivore	144	0.72	198	0.39	193	0.60	122	0.41
Woodborer	44	1.85	54	2.41	35	1.50	20	1.20
Predator	304	2.34	482	1.09	620	1.98	480	1.45
Omnivore	395	0.18	233	0.17	92	0.08	113	0.08
Trees with barriers								
Herbivore (aboveground)	62	0.10	93	0.65	72	1.07	71	3.01
Herbivore (belowground)	2	0.03	4	0.03	2	0.004	1	0.001
Detritivore	109	0.23	191	0.46	154	0.51	99	0.36
Woodborer	19	0.71	28	1.07	20	1.06	12	0.87
Predator	225	0.06	388	0.85	432	0.81	362	0.81
Omnivore	103	0.04	333	0.15	126	0.07	169	0.01

[a] Twenty-four traps were operated at each height and treatment (trees with or without barriers) except at mid-crown where only 2 traps tree^{-1} fit on the bole. Traps were operated continuously from September 1992 to September 1993 but only 1 weekly sample month^{-1} was examined.

Table 4
Total number and biomass (g oven-dried weight) of insects in various guilds captured in flight traps at different heights along the boles of eight longleaf pine trees[a]

Insect guild	Height of flight traps above ground (m)									
	1		4		7		10		13	
	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass (g)
Herbivore (aboveground)	112	0.424	99	0.381	143	0.700	139	0.846	153	1.073
Herbivore (belowground)	26	1.510	26	0.666	39	1.048	28	0.906	46	0.664
Detritivore	1018	1.033	653	1.75	625	1.404	612	1.045	718	0.92
Woodborer	161	0.621	137	1.052	93	0.699	99	1.803	88	0.257
Predator	228	0.706	207	0.766	189	1.851	186	0.732	208	0.868
Omnivore	114	0.097	57	0.048	21	0.013	24	0.032	16	0.009
Pollen-nectar	8	0.266	2	0.002	3	0.078	2	0.073	–	–

[a] Three traps tree^{-1} were operated at each height (24 traps height^{-1}). Traps were operated continuously from September 1992 to September 1993 but only 1 weekly sample month^{-1} was examined.

Although the arthropod diversity was similar for crawl trap captures regardless of height, the similarity of the arthropod fauna at different trapping positions varied (Table 7). For example, the similarity of trap captures at the base of the tree crown and mid-crown was 78.4% while the similarity at the base of the tree and the base of the crown was 50.7%. Thus, the composition of the community varied with height in the tree, although diversity was approximately the same at each trap position.

The percent similarity between flight traps at the base of the tree (1 m) and other locations on the tree bole was approximately 50% (Table 7). Arthropods captured in traps at 4 m and above were more similar.

Comparison of faunal similarity between pitfall, flight and crawl traps showed that pitfall and flight trap captures had the lowest similarity (Table 7). Arthropods captured in crawl traps and pitfalls had a 58% similarity, and comparison of flight traps to crawl traps without a barrier to arthropod movement showed a 60% similarity.

The addition of a barrier to the base of one-half of the trees with crawl traps caused a significant reduction in the biomass of arthropods captured. Barriers reduced arthropod biomass 75% at the base of the tree, 43% at mid-bole and 59% at the base of the crown (Fig. 1). Barriers had less of an effect on numbers of arthropods captured. Only captures in traps at the base of the tree were significantly ($P <$

Table 5
Total number of arthropod genera and diversity (H′) captured in crawl traps located at different heights on longleaf pine tree boles; one-half of the trees had barriers at their bases to prohibit arthropods from crawling from the ground onto the boles[a]

Trap position	Trees without barriers		Trees with barriers	
	No. of genera	H′[b]	No. of genera	H′[b]
Tree base	119	2.54	100	2.68
Mid-bole	117	2.71	121	2.69
Base of crown	108	2.82	96	2.65
Mid-crown	111	2.72	93	2.42

[a] Twenty-four traps were operated at each height and treatment (trees with or without barriers) combination except at mid-crown where only 2 traps tree^{-1} fit on the bole. Traps were operated continuously from September 1992 to September 1993 but only 1 weekly catch month^{-1} was examined.
[b] Shannon diversity index.

Table 6
Total number of insect genera and diversity (H′) captured in flight traps operated at different heights along the boles of 50–70-year-old longleaf pine trees[a]

Trap height (m)	No. of genera	H′[b]
1	226	3.25
4	188	3.39
7	183	3.32
10	165	3.38
13	133	2.97

[a] Traps were operated continuously during the period September 1992 to September 1993 but only 1 weekly sample month^{-1} was examined. Samples were collected in 24 traps at each height (3 traps height^{-1} tree^{-1}).
[b] Shannon diversity index.

Table 7
Raabe's percentage of similarity for arthropod fauna captured at different heights or in different types of traps operated for 1 year (September 1992–September 1993)

Comparisons	Percent similarity
Crawl traps	
Base to mid-bole	66.6
Base to base of crown	50.7
Base to mid-crown	52.1
Mid-bole to base of crown	67.4
Mid-bole to mid-crown	66.0
Base of crown to mid-crown	78.4
Flight traps	
1 m to 4 m	56.6
7 m	51.3
10 m	49.5
13 m	51.8
4 m to 7 m	69.9
10 m	70.1
13 m	58.4
7 m to 10 m	74.0
Between trap types	
Pitfalls to flight traps	10.4
Crawl to pitfall traps	58.1
Crawl to flight traps	60.1

0.05) reduced (by 49%). Barriers reduced arthropod biomass significantly in crawl traps, so we speculated that those trees would be the most likely to exhibit a trap-out effect if the remaining biomass resulted from resident species. However, regression analysis of arthropod numbers and biomass with the number of days after trap installation on those trees showed no significant correlation ($r^2 = 0.004$).

3.3. Seasonal variation

Seasonal abundance and biomass of arthropods captured in crawl traps was relatively high throughout the year except during March 1993 (Fig. 2). Biomass also was low in June in crawl traps, a time when high numbers of arthropods were captured. Flight traps exhibited a declining trend in numbers and biomass from October 1992 through March 1993, when both were very low.

Seasonal changes in arthropods collected by bark sampling showed a different trend. Although twice as many specimens were collected in summer bark samples (Table 8), there were no significant differences in the number of individuals collected per tree. However, the mean biomass of arthropods per tree was significantly higher in the winter than in the spring or summer. Fall and winter collections did not differ. Crawl traps captured their highest numbers and biomass in the fall; flight traps in the spring.

3.4. Vertical distribution

The distribution of arthropods on the tree boles was examined in crawl traps without barriers, flight traps and bark samples. Crawl traps caught equal numbers of arthropods regardless of position on the tree. Arthropod biomass also was relatively constant in crawl traps, although traps at the mid-crown position caught significantly less (Probability $> F < 0.04$) than those placed at the base of the crown (Fig. 1).

Flight trap position also had little effect on arthro-

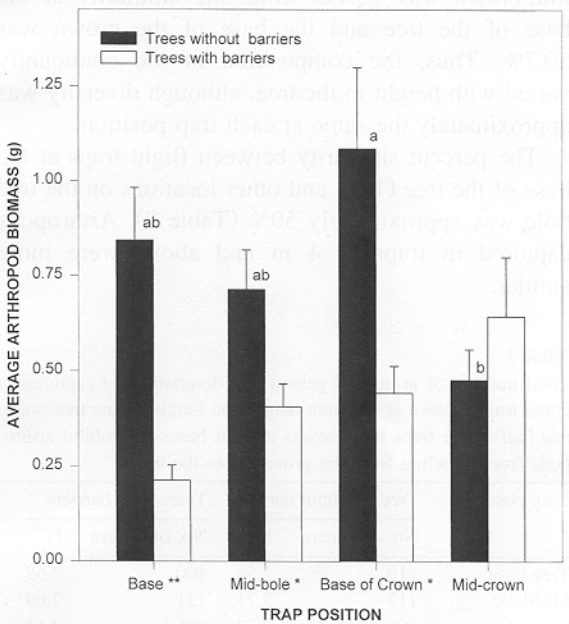

Fig. 1. Mean (⊤ 1 SE) biomass of arthropods captured in crawl traps on mature longleaf pine trees with and without a barrier to arthropod movement up the tree from the ground. Columns of the same color with the same letter are not significantly different by the Ryan-Einot-Gabriel-Welch multiple range test ($P < 0.05$). Asterisks denote that means of trees with barriers are significantly different (paired t-test; $^{*}P < 0.03$, $^{**}P < 0.002$) from those without barriers at a given position.

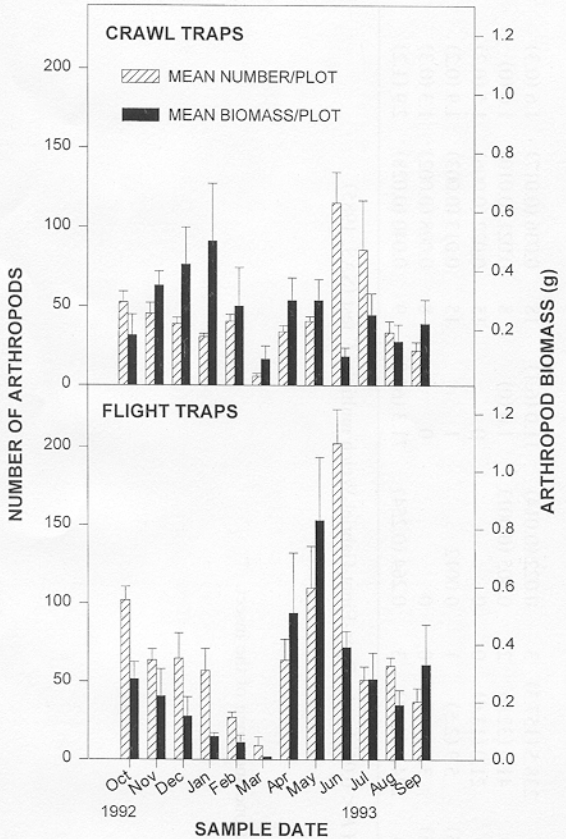

Fig. 2. Mean number and biomass (⊤ 1 SE) of arthropods captured on the boles of mature longleaf pines in crawl traps without barriers and flight traps by collection date. Samples were collected for 1 week per month.

pod numbers or biomass. The only differences (Probability $> F < 0.002$) were in traps at the base of the tree (217 insects tree^{-1}) which captured higher numbers of insects than traps at 7 m (137.8 insects tree^{-1}), 10 m (142.4 insects tree^{-1}) and 13 m (107.25 insects tree^{-1}).

Arthropod biomass in bark samples showed the same trend as crawl traps and flight traps (Table 9). However, the numbers of arthropods were much higher in samples collected from the base of the bole. Despite the high numbers of arthropods collected at that position, arthropod biomass was similar along the bole except in the mid-crown and live branches which were lower.

During the last 3 months of the study, dead branches were sampled from the crowns of the trees. Comparison of arthropod abundance and biomass in the dead branch samples to that in other locations on the trees showed that dead branches harbored as much arthropod biomass as the bark at the base of the tree (Table 9). Both positions had significantly more biomass and numbers of arthropods than the mid-bole, base of the crown or mid-crown.

Examination of how arthropod numbers and biomass were distributed among insect groups collected during bark sampling showed that the Hymenoptera were the most numerically abundant group (Table 10). This was primarily because of two ants, *Crematogaster* sp. and *Camponotus* sp. (Table 9). In Table 9, the numbers and biomasses of the three insects are the means of the samples that contained at least one specimen. For example, 27 samples of the 108 examined from the base of trees had an average of 161 *Crematogaster* sp. ants sample^{-1}.

Crematogaster sp. were found in high numbers in both the bark at the base of the tree and in dead branches in about one-third of the trees (Table 9).

Table 8
Mean number and arthropod biomass (g oven-dried weight) collected in various seasons of the year by three different sampling methods from the boles of mature longleaf pines

Season	Crawl traps[b]			Flight traps[b]			Bark samples[b]		
	N	Number[a]	Biomass[a]	*N*	Number[a]	Biomass[a]	*N*	Number[a]	Biomass[a]
Fall	13	303.2 (23.6)^{A}	2.59 (0.59)^{A}	13	78.5 (7.4)^{B}	0.24 (0.61)^{B}	39	61.8 (10.8)^{A}	0.23 (0.05)^{AB}
Winter	24	111.0 (19.0)^{B}	1.05 (0.90)^{B}	24	31.0 (6.4)^{C}	0.05 (0.01)^{B}	24	64.3 (19.1)^{A}	0.32 (0.05)^{A}
Spring	24	154.8 (20.7)^{B}	1.23 (0.18)^{B}	24	124.6 (16.6)^{A}	0.58 (0.11)^{A}	24	28.0 (13.0)^{A}	0.13 (0.02)^{B}
Summer	24	129.2 (29.6)^{B}	0.48 (0.09)^{B}	24	49.4 (4.7)^{BC}	0.27 (0.06)^{B}	23	132.4 (86.1)^{A}	0.12 (0.03)^{B}

[a] Means (1 SE) per plot per week of sampling.
[b] Means within columns followed by the same capital letter are not significantly different ($P < 0.05$) by the Ryan-Einot-Gabriel-Welch multiple F test (SAS, 1985).

Table 9
Mean arthropod biomass (g oven-dried weight) and number per sample extracted from bark scrapings or dead branches of longleaf pine; samples were collected for 12 months at the base of the trees, mid-bole, base of crown mid-crown and a live branch; samples of dead branches were collected for 3 months and compared to bark samples taken during those months

	All arthropods[a]			*Crematogaster* sp.[a]			*Camponotus* sp.[a]			Blattidae[a]		
	N[b]	Biomass[c]	Number[d]	N[e]	Biomass	Number	N[e]	Biomass	Number	N[e]	Biomass	Number
Sampled for 12 months												
Base	108	0.072 (0.016)^{A}	46.3 (18.8)^{A}	27	0.056 (0.019)	161.3 (71.0)	8	0.048 (0.022)	29.6 (13.3)	37	0.041 (0.008)	1.8 (0.17)
Mid-bole	110	0.041 (0.008)^{ABC}	9.2 (2.7)^{B}	15	0.014 (0.008)	39.7 (16.9)	3	0.003 (0.001)	1.0 (0)	37	0.035 (0.008)	1.6 (0.21)
Base of crown	110	0.047 (0.009)^{AB}	6.6 (1.3)^{B}	14	0.009 (0.006)	16.3 (8.3)	0	0	0	59	0.023 (0.003)	2.2 (0.32)
Mid-crown	108	0.036 (0.008)^{BC}	6.1 (1.2)^{B}	22	0.001 (0.0002)	4.3 (1.3)	3	0.002 (0.0002)	1.6 (0.7)	61	0.022 (0.003)	2.5 (0.36)
Live branch	110	0.013 (0.002)^{BC}	2.5 (0.3)^{B}	11	0.001 (0.0004)	2.5 (0.5)	2	0.003 (0.0006)	1.0 (0)	41	0.012 (0.002)	2.2 (0.38)
Dead branch	–	–	–	–	–	–	–	–	–	–	–	–
Sample period including dead branches												
Base	39	0.108 (0.041)^{A}	78.0 (50.2)^{A}	12	0.085 (0.041)	238.5 (157.3)	3	0.022 (0.014)	11.0 (6.1)	18	0.036 (0.017)	1.6 (0.3)
Mid-bole	39	0.018 (0.006)^{B}	8.4 (5.1)^{B}	6	0.008 (0.005)	41.0 (32.0)	2	0.005 (0.001)	1.0 (0)	8	0.021 (0.010)	1.0 (0)
Base of crown	39	0.026 (0.005)^{B}	6.9 (3.0)^{B}	8	0.013 (0.010)	21.0 (13.6)	0	0	0	15	0.022 (0.006)	1.5 (0.2)
Mid-crown	38	0.015 (0.003)^{B}	4.7 (1.0)^{B}	11	0.001 (0.0005)	5.9 (2.5)	1	0.0012	1	15	0.013 (0.003)	1.9 (0.2)
Live branches	39	0.010 (0.004)^{B}	1.6 (0.4)^{B}	2	0.001 (0.0005)	3.5 (2.5)	0	0	0	8	0.008 (0.002)	1.3 (0.3)
Dead branches	38	0.093 (0.031)^{A}	72.3 (21.9)^{A}	11	0.143 (0.034)	224.1 (49.3)	3	0.264 (0.254)	71.3 (65.9)	9	0.040 (0.028)	2.9 (1.2)

[a] Mean (1 SE) followed by the same capital letter are not significantly different ($P < 0.05$) by the Ryan-Einot-Gabriel-Welch multiple F test (SAS, 1985).
[b] N is the total number of samples collected.
[c] Data were transformed using a $\log_{10}$ transformation to stabilize variance.
[d] Data were transformed using a square root transformation to stabilize variance.
[e] N is the frequency of occurrence, i.e. the number of samples containing at least one specimen of the insect.

Table 10
Mean biomass (g oven-dried weight) and number of the eight most common orders of arthropods found in bark and dead branch samples from mature longleaf pines; means are the cumulative totals of each order per plot for all sample dates and positions

Order	N	Biomass[a]	Number[a]
Orthoptera	8	1.084 (0.199)^{A}	78.4 (13.1)^{B}
Hymenoptera	8	0.881 (0.163)^{AB}	1459.3 (369.5)^{A}
Coleoptera	8	0.648 (0.161)^{ABC}	55.6 (10.3)^{B}
Hemiptera	8	0.521 (0.133)^{ABCD}	11.6 (1.8)^{B}
Araneae	8	0.395 (0.039)^{BCD}	87.8 (8.0)^{B}
Lepidoptera	8	0.126 (0.033)^{CD}	4.9 (0.8)^{B}
Thysanura	8	0.068 (0.006)^{CD}	11.9 (1.5)^{B}
Geophilomorpha	8	0.041 (0.008)^{D}	8.3 (1.0)^{B}

[a] Means (1 SE) followed by the same capital letter are not significantly different ($P < 0.05$) by the Ryan-Einot-Gabriel-Welch multiple range test (SAS, 1985).

Camponotus sp. were only found in large numbers in the dead branches and to some extent in the bark at the base of the trees. Only three of 38 dead branches sampled contained *Camponotus* sp. while 11 contained *Crematogaster* sp.

The orders Orthoptera, Hymenoptera, Coleoptera and Hemiptera all had approximately the same biomass on the bark despite the very high number of Hymenoptera sampled (Table 10). The most common Orthoptera sampled were roaches in the genus *Parcoblatta*. Roaches were recovered from all sample locations in about equal numbers, but the biomass per sample declined with height, suggesting that roach size declined with increasing height in the tree (Table 9). However, dead branches contained larger roaches than live branches. This may have been due to the greater availability of holes, crevices and loose, sloughing bark on dead branches that provided better hiding places for larger roaches.

4. Discussion

This study shows that the bark of *P. palustris* hosts a large and dynamic macroarthropod community. This community includes resident species, such as *Crematogaster* sp. ants, bark lice (Psocoptera) and some spiders. Many species, such as wood roaches and some spiders and their predators the spider wasps (Hymenoptera: Pompilidae), utilize the bark as an integral part of their forest habitat needs. Others use the tree bole as a travel route or incidental resting place. This latter group includes two of the most commonly encountered insects in this study, the reproduction weevils, *H. pales* and *P. picivorus*. Although the larvae function as detritivores feeding on the stumps and roots of recently dead trees, the adults caught in our traps are herbivores that feed on the phloem of small branches in the canopy at night and return to the litter layer during the day (Nord et al., 1984). Both species are capable of flight, but adult weevils were frequently caught in crawl traps at all heights, suggesting that they often climb the tree bole to reach their feeding sites. Nicholai (1986) reported similar findings for a number of weevil species, and Moeed and Mead (1983) reported that a large variety of arthropods use the tree bole as a travel route to the canopy, including many weevils.

The number of arthropod genera captured on the bark was high. Over 220 genera were identified in flight traps at the base of the tree alone. Shannon diversity estimates were relatively constant over the bole of the tree in both crawl traps and flight traps, although the number of genera declined with height in flight traps but not crawl traps. Flight trap captures had a more diverse fauna than crawl traps both in terms of number of genera caught and Shannon diversity. The results from flight traps are consistent with those from a related study where flight traps were placed at three heights (New, 1995).

Despite the comparable diversity over the tree bole, faunal similarity between the base of the tree and mid-crown (13 m for flight traps) was only about 50% for both flight and crawl traps. Although the community associated with the base of the tree is as diverse as the community at mid-crown, the two communities differ somewhat in their composition.

Many of the arthropods captured on the bark are listed in New (1995) and Hanula and New (1996). These arthropods represent a range of functional roles. Herbivores were common on the bark, but for them the bark is little more than a resting site or a route to the canopy. Detritivores and omnivores also were common on the bark of live longleaf pine, but what benefit they derive from the bark is unclear.

Wood roaches are an important part of the detritivore/omnivore guild because they are a significant

part of the diet of nestling red-cockaded woodpeckers (Harlow and Lennartz, 1977; Hanula and Franzreb, 1995), and are probably important to adult birds as well. Like Hooper (1996), we found wood roaches distributed over the entire tree bole. Common in both crawl traps and bark samples, we found all stages of development from oothecae to adults. Because wood roaches are capable of eating a wide variety of foods (Rau, 1940; Gorton, 1980), they may be able to find sufficient food on the bark. In addition, the bark may provide protection from some predators or from harsh environmental conditions.

Knowledge about the habitat needs of the arthropods on the bark is critical to effectively manage red-cockaded woodpecker foraging areas. If the arthropods spend most of their time on the bark and rarely leave it, then current management practices that provide adequate bark surface in the right age or size classes are appropriate. However, if arthropods move readily between the bark surface and the forest floor or understory vegetation, and the latter two provide adequate or critical habitat needs (e.g. food), then managing only to provide sufficient bark surface may be inadequate.

Our study demonstrates that a large portion of the arthropod community on the bark is crawling up the tree from the forest floor or flying in from detritus or living vegetation. For example, crawl and pitfall traps had a 58% faunal similarity; crawl and flight traps 60%. Flight and pitfalls had only 10% similarity. Therefore, little of what flies to the bark spends time crawling on the ground. This similarity between what crawls on the forest floor and on the bark, coupled with our data that shows a barrier to arthropod movement up the tree significantly reduces arthropod biomass over most of the tree bole, is clear evidence that much of the biomass available to red-cockaded woodpeckers is climbing onto the tree from the soil/litter layer. Although the barriers reduced arthropod biomass in crawl traps by as much as 75%, we suspect that they were not completely effective in preventing some arthropods from gaining access to the tree bole. We base this suspicion on two findings: (1) that the barriers reduced biomass but did not affect the overall numbers of arthropods, and (2) the faunal similarity between trees with and without barriers was high (83%). In particular, barriers were not effective deterrents to wood roaches. Previous studies have shown that *Parcoblatta* sp. roaches are highly mobile and move readily throughout their forest habitats (Cantrell, 1943; Gorton, 1980), and Moeed and Mead (1983) concluded that the roaches captured in crawl traps on tree boles in New Zealand also were moving up from the ground.

Further evidence for the continuous exchange of arthropods between the bark and the remainder of the forest habitat is derived from 12 months of continuous trapping; during this time we saw no evidence of a depletion of the arthropods on the trees. If the arthropods we captured were more restricted to the tree bole in their habitat requirements, we might have observed a 'trap-out' effect where the numbers and biomass declined over time. However, no such trend was observed on trees that had barriers. Although maintenance of arthropod populations on the bark could be the result of reproduction by arthropods living there, we suspect that the constant influx of arthropods flying to the trees and crossing the barriers maintained the biomass at a relatively constant but lower level during the study.

Nicholai (1986) reported on the resident bark community, including the microarthropods, of six European tree species. He found relatively few true bark inhabitants and many residents species were microarthropods. Although microarthropods may be important in the food web on the bark, we did not consider them since they are probably not important prey of the red-cockaded woodpecker.

Seasonal variation in arthropods on the bark is important because red-cockaded woodpeckers are non-migratory. We found that arthropod biomass in bark samples was highest in the fall and winter, suggesting that the bark is also an overwintering site or a resting area where some arthropods can hide during cold periods which limit their activity. Crawl traps captured their highest arthropod biomass in the fall. In contrast, flight traps captured their greatest numbers and biomass of arthropods in the spring and their lowest in the winter. This low biomass of flying insects in winter is probably not vital to red-cockaded woodpecker survival, because previous studies show that they do not prey on large numbers of actively flying insects (Beal, 1911; Harlow and Lennartz, 1977; Hanula and Franzreb, 1995).

The arthropods captured in crawl traps and bark samples were the most similar to what red-cockaded

woodpeckers eat at the SRS (Hanula and Franzreb, 1995; Hanula, unpublished data). Our data on seasonal abundance and biomass collected by these two techniques are similar to the observations by Hooper et al. (1982) on changes in red-cockaded woodpecker foraging territory. They observed 24 bird groups and found that 71% of the foraging territory was used during the summer and 56% in the fall. Their summer period included much of our spring period and it also included the nestling period, a time when foraging territories were the smallest in their study. We found that both numbers and biomass were highest in crawl traps in the fall and lowest in the summer. Bark samples exhibited a similar trend but they had high biomasses in fall and winter. Fall bark samples had twice as much arthropod biomass as summer samples. However, due to variation among plots these differences were not significant. Skorupa and McFarlane (1976) reported smaller summer foraging territories compared to winter for two bird groups at the SRS. They did not observe birds in the fall. However, they point out that timber harvesting in foraging territories that occurred between observation periods may have affected the results.

Skorupa and McFarlane (1976) concluded that winter was a time of limited arthropod availability and that summer was a time of abundance. However, the seasonal arthropod biomass collected in the bark samples and monthly trap captures in this study suggest that red-cockaded woodpeckers do not experience prolonged periods of low arthropod availability on that strata. Any periods of low arthropod availability would probably occur in the summer months when we noted the lowest arthropod biomasses and when Hooper et al. (1982) observed increased size in foraging territories. However, red-cockaded woodpeckers may compensate for the lower summer arthropod biomass on the bark by foraging on dead branches of live trees and occasionally on the boles of dead trees (Ligon, 1970; Baker, 1971a; Hooper and Lennartz, 1981). These two foraging substrates are less likely to exhibit large seasonal variations in arthropod biomass, although dead trees may not always be available. Red-cockaded woodpecker also forage on wild cherry (*Prunus serotina*), wax myrtle (*Myrica cerifera*), blueberry (*Vaccinium* sp.), sweet bay (*Magnolia virginiana*) and poison ivy (*Rhus radicans*) fruit (Baker, 1971a; Hooper and Lennartz, 1981), so they may be able to use fruits and seeds to supplement their arthropod diet.

Our data support others (Moeed and Mead, 1983; Nicholai, 1986) in showing that bark is an integral part of the forest ecosystem and that relatively few macroarthropods live exclusively on or in the bark. Instead, the arthropod community on the bark appears to be in constant flux, with a large portion of the community coming from the soil/litter layer and a diverse fauna flying to the bark surface.

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